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RESEARCH ARTICLE

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Cascading effects of climate variability on the breeding success of an edge population of an apex predator

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Abstract

1. Large-scale environmental forces can influence biodiversity at different levels of biological organization. Climate, in particular, is often associated with species distributions and diversity gradients. However, its mechanistic link to population dynamics is still poorly understood.
2. Here, we unravelled the full mechanistic path by which a climatic driver, the Atlantic trade winds, determines the viability of a bird population.
3. We monitored the breeding population of Eleonora's falcons in the Canary Islands for over a decade (2007–2017) and integrated different methods and data to reconstruct how the availability of their prey (migratory birds) is regulated by trade winds. We tracked foraging movements of breeding adults using GPS, monitored departure of migratory birds using weather radar and simulated their migration trajectories using an individual-based, spatially explicit model.
4. We demonstrate that regional easterly winds regulate the flux of migratory birds that is available to hunting falcons, determining food availability for their chicks and consequent breeding success. By reconstructing how migratory birds are pushed towards the Canary Islands by trade winds, we explain most of the variation (up to 86%) in annual productivity for over a decade.
5. This study unequivocally illustrates how a climatic driver can influence local-scale demographic processes while providing novel evidence of wind as a major determinant of population fitness in a top predator.

KEYWORDS

bird migration, forward trajectory model, predator–prey interactions, trade winds, wind-driven food availability

1 | INTRODUCTION

Climate strongly shapes the distribution and dynamics of biodiversity on Earth. Spatial variation in climatic conditions affects broad-scale distribution patterns, such as biome composition (Gaston, 2000) and the latitudinal gradient of diversity (Willig, Kaufman, & Stevens, 2003), whereas temporal variation drives range expansions, contractions and shifts (Lenoir & Svenning, 2015), as well as seasonal changes in

population distributions (e.g. animal migration, Dingle, 2014). To understand how climate affects different facets of biodiversity, we need to understand how climatic variability affects populations, and ultimately shapes the dynamics of species, communities and ecosystems (Kearney & Porter, 2009; Leroux et al., 2013; Stenseth et al., 2002; Thackeray et al., 2010). Climatic variability affects population dynamics in different ways, either directly by impacting vital rates (Coulson et al., 2001) or indirectly by affecting community composition and interactions through effects on predators, pathogens, competitors and, most notably, resource availability (Boggs & Inouye, 2012). For example, temperature shifts and fluctuations might cause phenological mismatches between resources and consumers at different trophic levels, as observed in waders (Pearce-Higgins, Dennis, Whittingham, & Yalden, 2010), songbirds (Both, Bouwhuis, Lessells, & Visser, 2006), seabirds (Durant, Anker-Nilssen, & Stenseth, 2003), and mammalian herbivores (Post & Forchhammer, 2008) and predators (Molnár, Derocher, Thiemann, & Lewis, 2010).

However, beyond the effect of local weather impacts, the mechanisms that underlie the effects of climatic variability on population dynamics remain poorly understood (Boucher-Lalonde, Morin, & Currie, 2016; Brown, 2014). Relating climatic variability to population responses is often hampered by the complexity of processes that ultimately link two very different scales: large-scale environmental drivers (e.g. climate) and local-scale biological phenomena (e.g. population response). Moreover, disentangling climatic drivers is challenging due to their complexity and interaction with multiple aspects of the biophysical environment. Temperature and precipitation have received much attention (Parmesan, 2006; Walther et al., 2002), though other climatic variables might have equally important roles. Regional and seasonal wind regimes can affect resource distribution and individual behaviour. For example, wind affects the distribution and abundance of flying insects, and can therefore affect the phenology (Irons et al., 2017), breeding performance and survival of insectivorous birds (Møller, 2013). Wind also influences the foraging strategies of flying animals, for example in large seabirds (Shamoun-Baranes, Bouten, van Loon, Meijer, & Camphuysen, 2016; Suryan et al., 2008). Moreover, changes in long-term wind patterns have been shown to correlate with foraging effort and breeding success of albatrosses (Thorne et al., 2016; Weimerskirch, Louzao, de Grissac, & Delord, 2012), ultimately determining their global distribution (Suryan et al., 2008). However, the establishment of causal links beyond correlations between wind and population responses has thus far been elusive.

Here, we investigated how the life-history strategy and viability of a population of Eleonora's falcon *Falco eleonorae* breeding in the Canary Islands, the edge of the species' range, is determined by a broad-scale climatic phenomenon—the Atlantic trade winds, which is the most consistent wind system on Earth (American Meteorological Society, 2020). The Eleonora's falcon is a long-distance migratory raptor that breeds over the entire Mediterranean basin and winters in Madagascar (Kassara et al., 2017; Walter, 1979). Its reproductive system is a striking example of adaptation by a highly specialized predator to exploit seasonal pulses of prey availability. We hypothesized that this predator–prey dyad is maintained by trade winds, and that wind patterns affect the breeding performance of the falcon population (Figure 1). During the breeding season, the Eleonora's falcon is highly specialized in hunting migratory birds that are intercepted over the ocean while heading to Africa. Consequently, falcon breeding colonies are strategically located across the main migratory flyways that connect Europe to Africa (Walter, 1979), and their timing of breeding (July–October) is synchronized with the peak in songbird autumn migration. Many trans-Saharan migrants from Western Europe migrate in a south-westerly direction to the Iberian Peninsula, and continue their flight along the West African coast to reach their wintering grounds in tropical Africa (Adamík et al., 2016; Hilgerloh, 1989; Ouwehand & Both, 2016). Long-term field and radar observations of autumnal migration from the southern Iberian Peninsula (Hilgerloh, 1988) and the close relationship between the wind regime and falcon hunting distances (Viana, Gangoso, Bouten, & Figuerola, 2016) suggest that food availability for the Canarian population of Eleonora's falcon strongly depends upon Atlantic trade winds, which are the prevailing northeasterly winds along the coast of Northwest Africa (Johnson & Stevens, 2000). Using a decade of observations, we investigated how the wind regime along the migratory route of birds migrating from the southern Iberian Peninsula affects

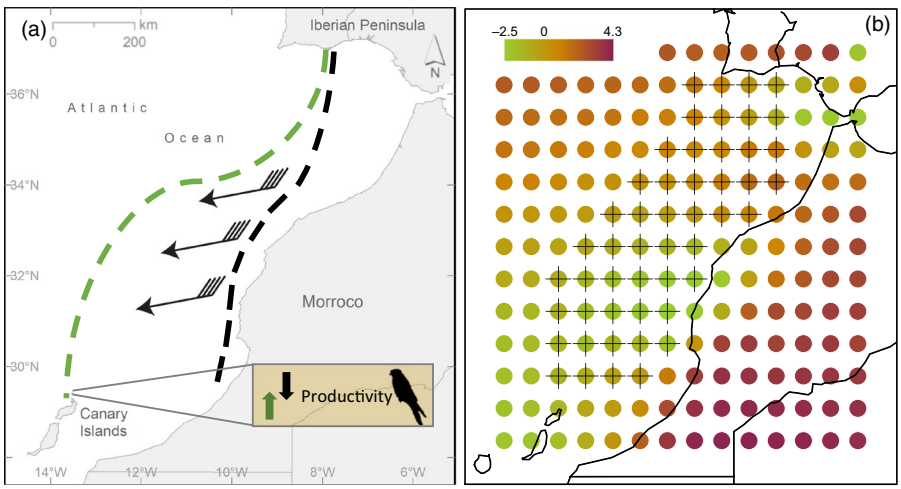

FIGURE 1 Main hypothesis of the study. (a) We hypothesize that Atlantic trade winds push migrating birds from their route along the African coast (black dashed line) in westward direction (green dashed line), and thus control food availability and breeding success of the Eleonora's falcon population of the Canary Islands. (b) Mean intensity of easterly winds (u-wind component) during September across the whole study period (2007–2017). The colour scale indicates the intensity of u-wind, with negative values corresponding to winds blowing from the East. Crosses delimit the hypothesized migration pathway

predator–prey interactions, and consequently the fitness of this highly specialized predator.

2 | MATERIALS AND METHODS

2.1 | General analytical approach

We used a spatially explicit, individual-based forward trajectory model and bird migration intensity and flight direction observed by weather radar to assess the effect of wind on food availability (migrating songbirds) for falcons. The model reconstructs the trajectories of songbirds departing from Southern Iberian Peninsula as a function of the wind conditions experienced *en route*, and provides quantitative data on the number of migratory birds reaching the vicinity of the falcons' breeding grounds. The model predictions were tested using long-term field monitoring data on the presence of fresh prey at the breeding grounds. To better understand how falcons deal with spatiotemporal changes in wind-driven food availability, we tracked 12 males (the food provisioning sex) with GPS between 2012 and 2017. To determine the effect of wind-driven changes in food availability on the falcons' breeding success, we related prey availability during the chick-rearing period (September) with the number of fledged offspring each year.

2.2 | Study area

Fieldwork was conducted from July to October each year, from 2007 to 2017, in Alegranza (29°24′N, 13°30′W, 10.5 km^2, 289 m a.s.l.), which is the northernmost island of the Canary archipelago and is located 170 km west of the African coast. The Canary Islands (27°37′ to 29°25′N, 13°20′ to 18°20′W) straddle the subtropical high-pressure belt (around 30°N) at the northern poleward edge of the Hadley Cell (Fernandopullé, 1976), which is a primary circulation wind cell that operates between zero and 30–40°N. The Azores semi-permanent high-pressure system influences the weather and climatic patterns of vast areas of North Africa and southern Europe. In the Canary Islands region, prevailing northeasterly trade winds driven by this high-pressure system dominate below ~1,500 m a.s.l. (Carrillo, Guerra, Cuevas, & Barrancos, 2016). Trade winds are highly dependent upon large-scale atmospheric circulation dynamics in the Atlantic Ocean, and variations in the NAO index (normalized pressure difference between the Azores high and the Icelandic low atmospheric pressure centres) positively correlate with variations in trade wind speed over land and ocean in the Canary region (Azorin-Molina et al., 2018). In addition, trade wind variation is coupled to the southern shift and strength of the Azores high-pressure system (Cropper, Hanna, & Bigg, 2014). During July–August, the Azores high reaches its northernmost position, and generates trade winds between 20° and 32°N latitude. In autumn, the Azores high moves south, so trade winds begin to move southwards until they reach their southernmost position in winter. Therefore, the strength of trade winds is generally strongest in summer and early autumn at the latitude of the Canary Islands (Figure 1), which perfectly matches the Eleonora's falcon breeding season.

2.3 | Population monitoring

The Eleonora's falcon colony on Alegranza consists of an average of 127 breeding pairs, which represents 45% of the total Canarian breeding population (Gangoso & Figuerola, 2019). The population has been monitored every year from 2007 to 2017. A total of 1,008 nesting attempts (range = 73–106 nests/year) were monitored on at least two occasions each year, first to quantify clutch size, and second to determine the final number of fledged offspring. Mean annual productivity was estimated as the number of fledglings divided by the number of breeding pairs monitored. As a general phenomenon and under intense migratory fluxes, Eleonora's falcons hunt as much as they can and, after feeding, store the subsequent leftover prey in larders located in caves and bushes around the nest site (Viana et al., 2016). Therefore, finding stored prey can be considered as indicative of food excess at population level rather than an individual behaviour. During each visit, we recorded the presence of fresh prey within a 5-m radius of the nest site by inspecting the nest and nearby larders. From these field observations, we created a continuous variable (number of fresh prey items per number of nests visited) that quantifies the abundance of fresh prey on the island.

2.4 | Wind data

We extracted wind data from ERA-interim reanalysis that was produced by the European Center for Medium-Range Weather Forecasts (ECMWF; Dee et al., 2011) at the 925-mb pressure level (roughly 750 m a.s.l., corresponding to the median altitude of nocturnal migrating passerines, Klaassen & Biebach, 2000). Wind data (the west–east, *u*, and south–north, *v*, components, m/s) were available every 6 hr at a spatial resolution of 0.75 × 0.75°. Data were extracted from 182 grid cells encompassing an area between Southern Iberia and the Canary Islands (i.e. wind grid, Figure 1) for the period 01–30 September 2007–2017.

2.5 | Migratory flux estimated by weather radar

Songbird migration intensity was observed by the weather radar of Loulé/Cavalos do Caldeirão (southwestern Portugal, 37°18′N, 7°57′W), which is located within the departure area of many trans-Saharan migrants that are heading to Africa (Nilsson et al., 2018). We analysed polar volume data of reflectivity and radial velocity that were obtained between 15 August and 15 October 2007–2016 (data from 2017 were unavailable). However, for further analyses, we only used data from September, as this is the chick-rearing period in Eleonora's falcons. The radar volume data were processed

into vertical profiles of birds following the procedures described by Dokter et al. (2010) using the vol2bird algorithm available in R package bioRad (Dokter et al., 2018). Bird profiles were calculated from samples within a range of 5–35 km from the radar position. The radar's sparse volume coverage pattern required us to use relatively wide altitude bins (500 m). To convert reflectivity measurements into bird densities, we assumed a radar cross-section per individual of 11 cm^2, following Dokter et al. (2010). For each night of migration, we analysed data from sunset to 4 hr after sunset, which should encompass most take-offs of trans-Saharan nocturnal migrants (Åkesson, Alerstam, & Hedenström, 1996). Profiles were calculated in 10-min interval. As additional quality control, bird densities in profiles with substantial rain, defined as profiles where half or more of the 0–4,000 m altitude column showed reflectivity factor >7 dBZ (quantity DBZH in bioRad), were set to zero. Finally, vertical migration profiles were plotted and manually inspected to verify absence of rain contaminations (Dokter et al., 2018).

Bird densities and speeds were integrated over height into a migration traffic rate (MTR, birds km^{-1} hr^{-1}), which was defined as the number of birds that passed a theoretical 1-km transect perpendicular to the direction of movement over 1 hr (Dokter et al., 2018). Average nightly MTR was calculated as the mean MTR from sunset to sunset +4 hr. Bird migration heading was calculated from the migration ground speed vector and wind vector for that period (Dokter, Shamoun-Baranes, Kemp, Tijm, & Holleman, 2013). Missing data from 2017 and missing values associated with radar maintenance tasks ($N = 49$ days in total) were filled by data imputation through a random forest algorithm. We used wind data (u and v daily means) for the four grid cells closest to the radar location and the proportion of arriving birds estimated from the trajectory model (see below) as predictor variables to impute MTR. The performance of data imputation was assessed using the normalized root mean squared error (NRMSE; Oba et al., 2003), which ranges from 0 (the best performance) to 1 (the worst performance). In our case, NRMSE was 0.30.

2.6 | Forward trajectory model

The forward trajectory model by Shamoun-Baranes and van Gasteren (2011) was used to calculate the daily number of migratory birds arriving to the falcons' breeding grounds. The model simulates individual birds that depart at sunset from the southwest coast of the Iberian Peninsula and fly with a constant airspeed and heading, while being drifted by the wind conditions experienced *en route*. The model used a fixed, 30-min forward-integration scheme and at each time step, the ground speed and track direction were calculated given the bird's airspeed, heading, and interpolated wind conditions at that specific point in space and time. We assumed an air speed of 10 m/s (Bruderer & Boldt, 2001) for migrating birds and used wind conditions at the 925-mb pressure level across the above-described wind grid. The mean heading of the birds was obtained from the weather radar data (see *Migratory flux*), calculated as the circular mean heading of all nights, weighted by MTR (208.4°). We allowed random variation using a normal distribution with a standard deviation of ±5° to account for individual variation in heading. Birds may partially compensate the effect of side winds experienced *en route* (see, for instance Shamoun-Baranes & van Gasteren, 2011) and this could ultimately affect the numbers of birds arriving in the Canary Islands. However, there is no evidence for compensation in nocturnal migrants over such long ocean crossings. And even if birds compensate to some extent, we do not expect differences in the relative number of birds arriving each day. Consequently, we decided not to add this behavioural complexity to the trajectory model.

For each night, we simulated the flight of nocturnal migratory birds departing at sunset from a 250-km wide area in the southern Iberian Peninsula (Figure 2). The number of departing birds (i.e. migration intensity) was obtained by integrating the MTR over the first 4 hr after sunset and assuming the radar measurement to represent the MTR over the full 250 km. To test the effect of other potential spatial distributions at departure, we also simulated west-skewed, east-skewed, and central distributions of departing birds along this 250-km band. Because these distributions led to almost similar results (see Table S1 and Figures S5–S7 detailed further below), we used the uniform distribution for further analyses. To work with manageable computational times, we simulated 10,000 birds each night, which was sufficient to obtain stable model outputs (see Figure S1). Note, the minimum number of birds observed (with radar data) departing in one day across the whole decade was 20,417, more than the double of simulated birds.

Simulations continued until birds reached the latitude of Alegranza (29.4°N) with a maximum of 30 hr after departure. For each day, we calculated the number of prey arriving within −14°W and −13°W longitude (about 50 km at each side of Alegranza), the distances of birds to Alegranza and the median distance of the closest 5% of migratory birds that arrived on Alegranza. Birds needed a mean of 20 hr ± 4.16 *SD* to reach this area. Therefore, the number of birds that arrived each day in Alegranza was calculated as the product of the proportion of birds within the defined longitudes as estimated by the trajectory model and the intensity of departure measured by radar (MTR) the day before. We assessed whether both the intensity of departing birds (squared root-transformed MTR) and the number of birds arriving at Alegranza (log-transformed) as estimated from the trajectory model varied significantly among years by performing ANOVA. We confirmed the results of the trajectory model with field observations by performing a Spearman correlation between the observed number of fresh prey on Alegranza and the predicted daily number of migratory birds arriving on the island.

2.7 | Falcons' movement

We tagged 12 adult male and 14 adult female Eleonora's falcons with 7.5-g solar-powered GPS trackers (www.UvA-BiTS.nl; Bouten, Baaij, Shamoun-Baranes, & Camphuysen, 2013) during the breeding seasons of 2012, 2014 and 2017. However, we analysed only data from male falcons because they are the food provisioning sex in this species (Walter, 1979). Geographical positions were recorded at intervals

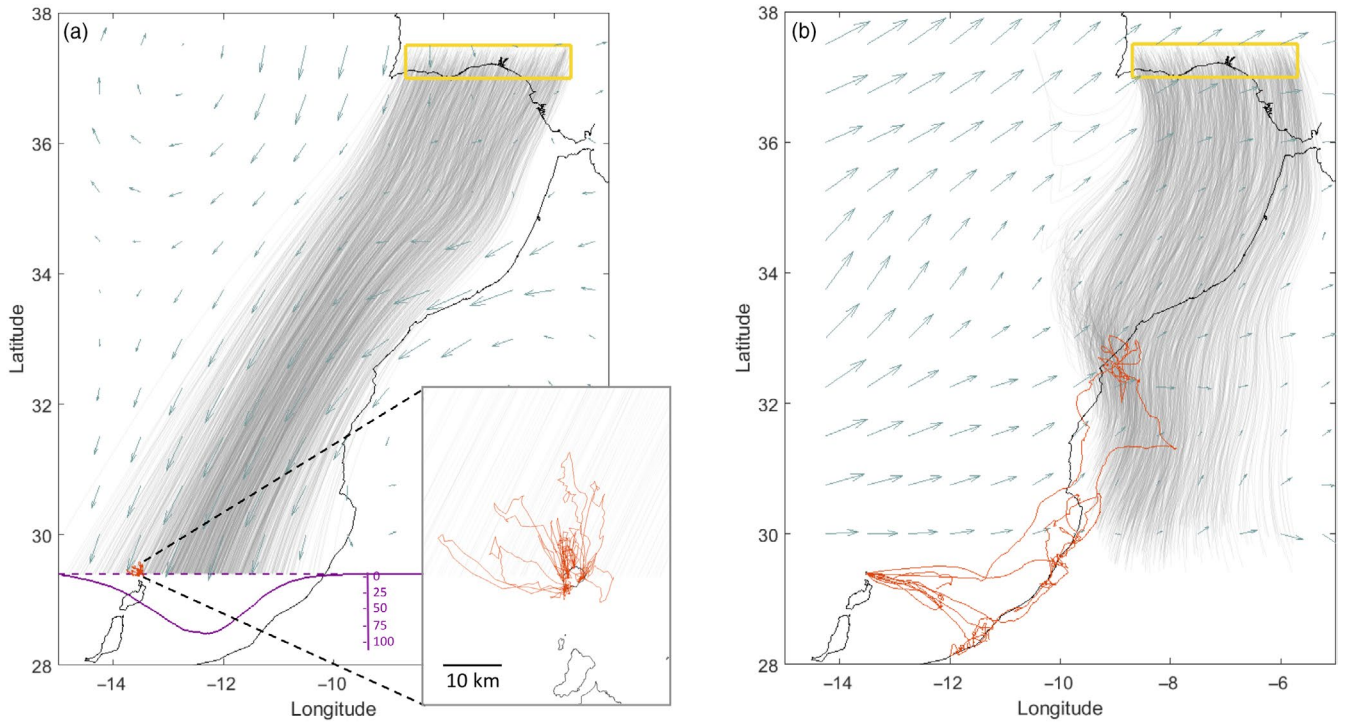

FIGURE 2 Wind conditions drive food availability for Eleonora's falcons in the Canary Islands. The distance of the migratory flux to the falcons' breeding grounds depends upon the prevailing wind conditions. The figure shows the simulated trajectories of migratory birds departing from a 250-km band in the southern Iberian Peninsula (yellow square) and the wind conditions encountered *en route* (dark green arrows). The purple line represents the frequency distribution of the longitudes of the trajectories of migratory birds at the latitude of Alegranza. The first example (a) corresponds to migratory birds departing on the 26 September 2017 after sunset and arriving on the 27 after a mean travel time of 19.29 hr. Eleonora's falcons hunting movements (orange lines, $N = 6$ males) correspond to the 27 September and are shown in detail in the zoomed panel. With favourable easterly winds, a dense flux approaches the archipelago and falcons just need to perform short hunting trips over the ocean to find their prey. However, the accessibility of migratory birds decreases and the distance and duration of hunting trips increase when winds blow from the west (b). In this extreme example, we show the trajectories of birds departing on the 14 September 2014 with winds that are also representative of the days to follow. When extreme adverse wind conditions prevail, the migratory flux is unreachable for hunting falcons, which may reach mainland Africa for self-maintenance

that ranged from 3 to 60 s, with a precision of 3–15 m. We removed GPS outliers with trajectory speeds greater than 80 m/s. We defined a 'foraging trip' as the first GPS location out of a 0.5-km buffer around the island (to exclude casual flights near the island perimeter) to the first location back in the 0.5-km buffer. For each foraging trip, we calculated the maximum distance from Alegranza and the duration of foraging flights (see R code in Gangoso et al., 2020). To directly link both the number of fresh prey on Alegranza (see below) and falcons movements to wind speeds, we used wind data from 18:00 UTC (departure) to 18:00 UTC of the following day (arrival). The average daily distance and duration of the trips were related to the daily wind direction using ANOVA, and related to the availability and distance of simulated tracks of migratory birds using Spearman rank correlations.

2.8 | Relationships between wind and food availability at breeding grounds

Prey availability was hypothesized to depend upon winds along bird migration routes from southern Iberia to the Canary Islands. Therefore, we related the wind conditions in the 50 grid cells encompassed by the hypothetical migration pathway (Figure 1) to the number of fresh prey on Alegranza by fitting a linear model (LM) where the number of fresh prey (log-transformed) was included as the response variable and the mean annual *u*- and *v*-wind components during September for each grid cell were included as explanatory variables. The north–south wind component (*v*-component) was not significant ($p = 0.39$) and was therefore removed from the model. In addition, we fitted independent LMs for each cell of the whole wind grid (182 grid cells), where the mean annual *u*-wind component was included as the explanatory variable to explore where the wind was most strongly associated to prey availability in Alegranza.

2.9 | Relationships between wind-driven food availability and falcons' breeding success

We assessed the relationship between wind conditions during September and the average number of fledglings produced by falcons each year from 2007 to 2017 (i.e. annual productivity). We considered three different explanatory variables: (a) the mean annual

easterly wind intensity (mean u-wind values) across the migratory path (Figure 1), (b) the mean annual food availability estimated by the trajectory model and (c) the maximum number of consecutive days with low food availability (i.e. food gap). To calculate the length of the food gap, we first deduced the prey number threshold below which food availability is insufficient to maintain chick growth and survival. Because we lack information for calculating such physiological limit, we heuristically checked which number of prey arriving per day (i.e. threshold) and associated food gap provided the best explanatory power (i.e. the R^2) of variation in productivity. This was done by progressively increasing the threshold value from 1,000 to 1 million birds, and calculating the R^2 of the relationship between the respective food gap and productivity. We found a clear unimodal pattern, with the explanatory power peaking at ~22,000 birds (Figure S2)—this value was chosen as the threshold. Because the different explanatory variables (a–c) were highly correlated (>0.64), we fitted separate models for each explanatory variable. For the relationships (a) and (c), we fitted linear models, and for the relationships (b) we fitted an exponential function using least squares. In addition, we assessed whether the NAO index (Jones, Jonsson, & Wheeler, 1997) during September, defined as the normalized sea-level pressure between Gibraltar and Reykjavik as obtained from the Climate Research Unit (available at https://crudata.uea.ac.uk/cru/data/nao/), was related to the falcons' productivity by using a *t* test. All the statistical analyses were performed in R v 3.4.3 (Team, 2017). See Gangoso et al. (2020) for the R-code and the specific packages used.

3 | RESULTS

3.1 | Wind conditions drive food availability

The observed number of fresh prey on Alegranza depended upon wind patterns along the migration pathway between Iberia and the Canary Islands. Although the winds are highly correlated along the pathway due to dominant climatic forces underlying the trade winds, the wind effect was stronger (i.e. higher R^2) over the sea, halfway along the migration pathway (Figure S3). The higher the intensity of easterly winds in the migration pathway (i.e. the more negative *u*-component), the greater the probability that migratory birds are hunted and stored by falcons (estimate ± *SE* = −0.14 ± 0.02, $p < 0.001$, $R^2 = 0.34$). The forward trajectory model also indicated that the wind conditions experienced *en route* can actually push migrating birds towards the Canary Islands (Figure 2). Simulated arrivals of migrants were confirmed by the field observations of fresh prey ($\rho = 0.48$, $p < 0.001$). Therefore, both the field data and the simulation model independently support the hypothesis that wind drives food availability for falcons during the breeding season.

3.2 | Falcons adjust hunting effort to maximize food supply

Male falcons performed hunting flights over the ocean with maximum distances of up to 140 km away from Alegranza. The distance and duration of hunting trips increased when migrating birds were passing farther from the breeding grounds (Figure 2b). The falcons travelled greater distances in search of food when the wind was blowing from the west (i.e. positive *u* component) compared to wind blowing from the east (i.e. negative *u* component; $F_{3,2,906} = 57.16$, $p < 0.001$; post hoc Tuckey test: $p_{SE\text{-}NE} = 0.02$, $p_{SW\text{-}NE} < 0.001$, $p_{NW\text{-}NE} < 0.001$, $p_{SW\text{-}SE} = 0.005$, $p_{NW\text{-}SE} = 0.08$, $p_{NW\text{-}SW} = 0.14$, Figure 3a). Hunting distances were negatively associated with the number of migratory birds within a 50-km radius from Alegranza ($\rho = -0.37$, $p < 0.001$), so the falcons did not need to travel long distances when the density of songbirds near the island was high (Figure 3b). Indeed, both the maximum distance travelled and the duration of hunting trips were positively associated with the distance of the migratory birds to Alegranza ($\rho = 0.37$, $p < 0.001$ and $\rho = 0.36$, $p < 0.001$, respectively). During prolonged periods of unfavourable wind conditions, male falcons reached the African mainland, at least 200 km from Alegranza (Figure 2b), where they stayed for up to 10 days.

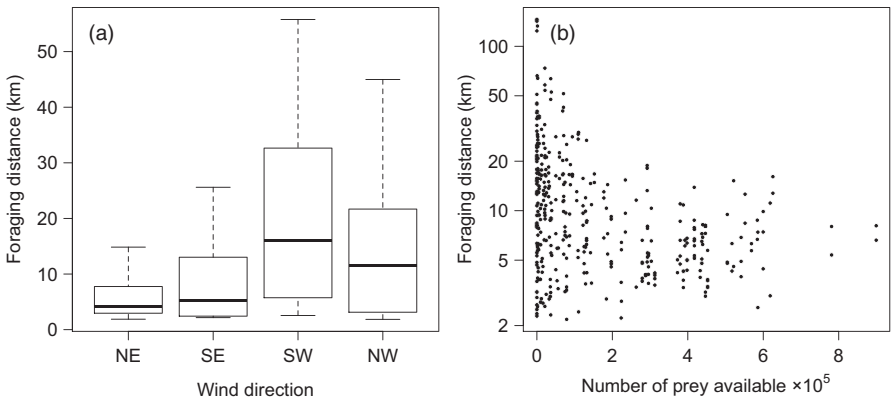

FIGURE 3 Eleonora's falcons cope with variations in food availability by adjusting their hunting effort. (a) Foraging distance under different wind directions in the migratory pathway. The lines within the boxes indicate the median, the edges of the boxes the first (Q1) and third (Q3) quartiles, and the whiskers extend to 1.5 times the interquartile range. Extreme values have been omitted for visualization purposes. (b) Maximum foraging distances as a function of prey availability near Alegranza

3.3 | Wind controls breeding performance

The intensity of favourable, easterly winds during September was strongly associated to the annual productivity (Fitted model: productivity = 1.13 − 0.35 × wind, $p < 0.001$, $R^2 = 0.78$, Figure 4a,b), with an increase in productivity of 0.84 by an average increase of 1 m/s in easterly winds. The effect of wind was higher over the sea and along the migratory pathway (Figure 4a), which clearly affected the availability of food. Although the intensity of the migratory flux as measured by the weather radar at the departure site was similar across years ($F_{10,319} = 1.85$, $p = 0.05$; 2016 was the only year that showed significantly lower flux, see Figure S4), the number of birds arriving on the Canary Islands as estimated by the trajectory model strongly varied among ($F_{10,319} = 4.43$, $p < 0.001$) and within years (see Figure 5 and Figure S5 for daily patterns using the four possible distributions of departing birds). This was reflected in the mean number of birds available

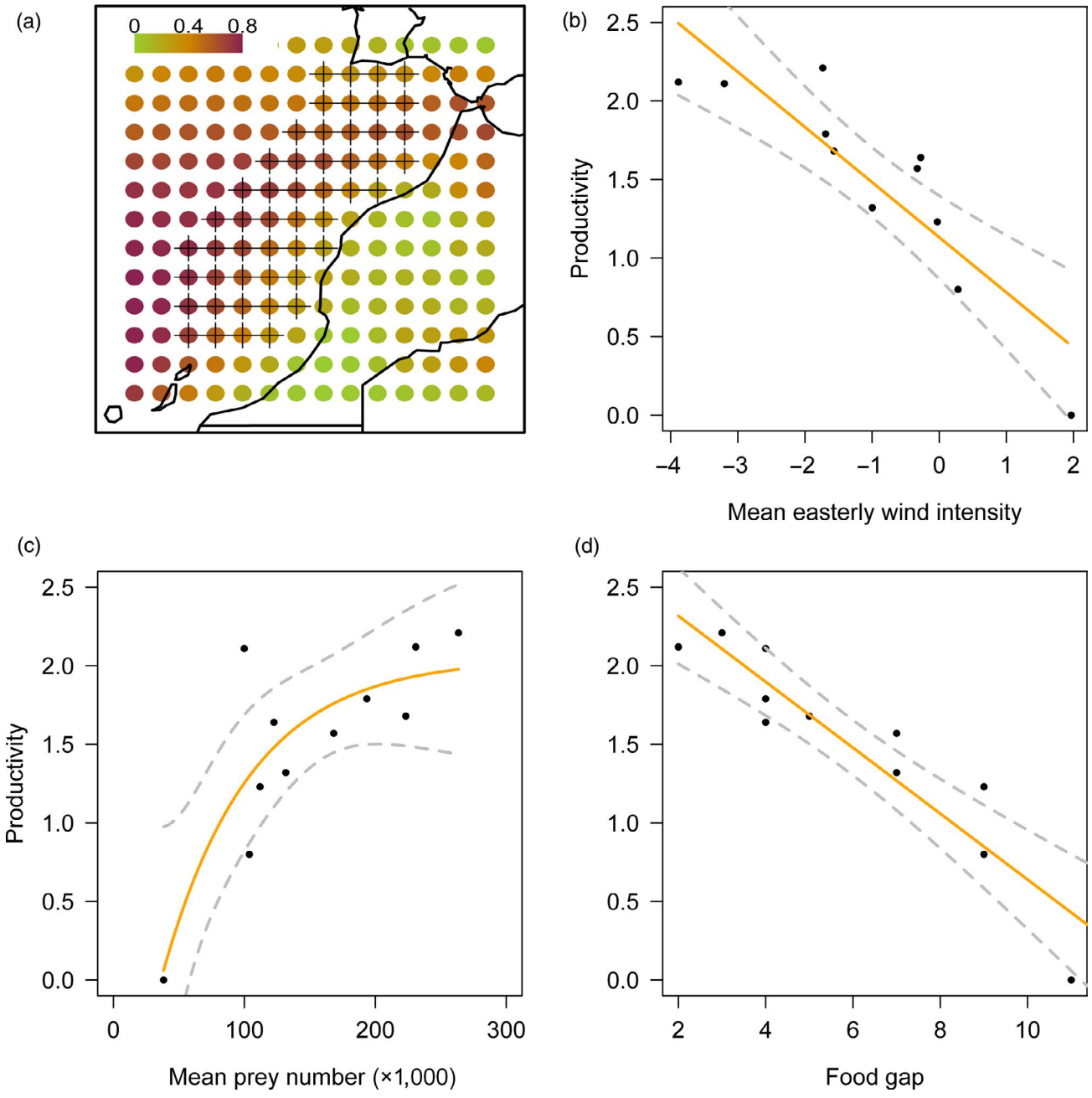

FIGURE 4 Relationships between annual productivity and (a, b) the annual mean intensity of easterly winds (*u*-wind component) during September, (c) the annual mean number of bird prey available and (d) the number of consecutive days without enough food (food gap) during September. The map (a) represents the R^2 (colour scale) of the relationship between productivity and annual mean easterly wind in each cell. Crosses delimit the hypothesized migration pathway. In panel (b), the same relationship is plotted using the mean easterly wind across the indicated migration pathway. The dashed lines in (b)–(d) represent the 95% confidence intervals. See Figure S6 for results considering other spatial distributions of departing birds

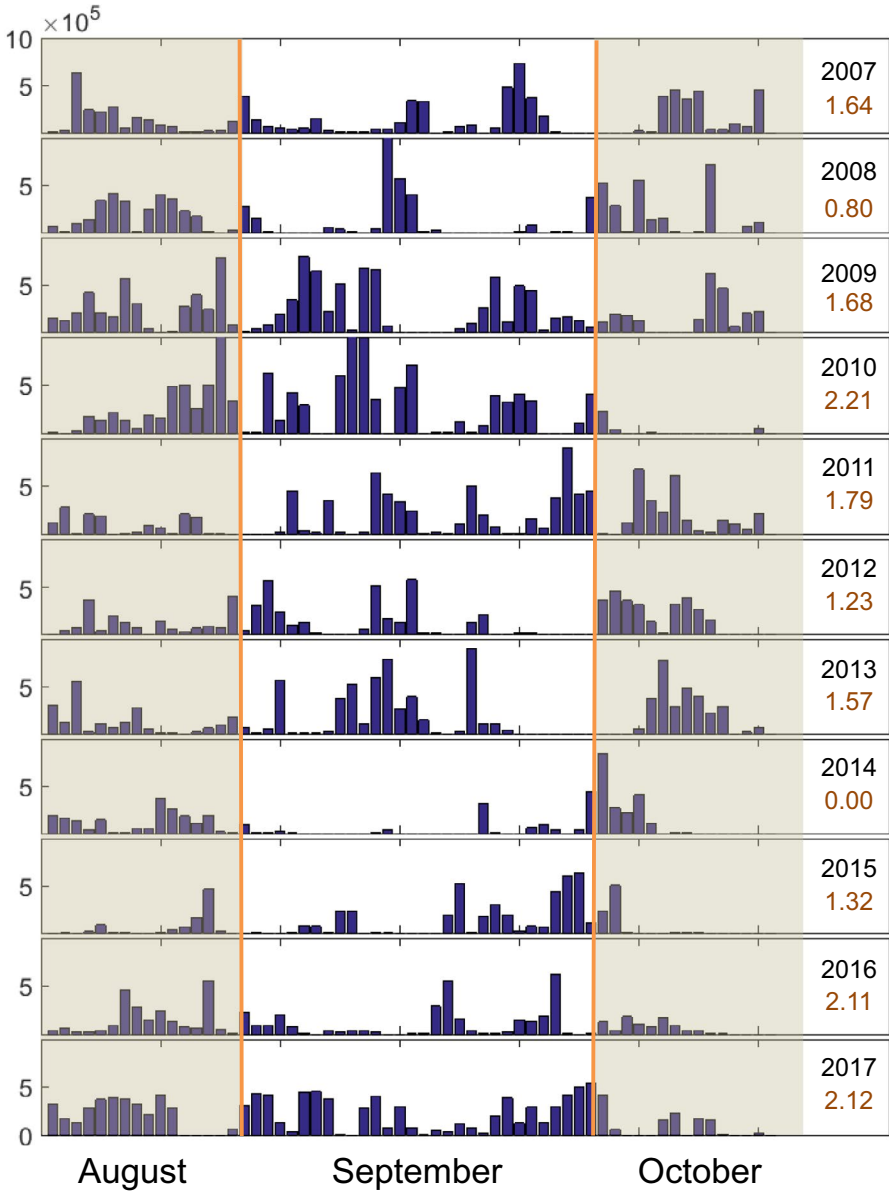

FIGURE 5 Number of birds arriving in Alegranza per day (September is delimited by the orange lines), as estimated from the trajectory model and radar data. Data from August and October are also shown to provide a wider overview of the variability in food availability across years. The year (black letters) and the corresponding productivity value (dark orange letters) are shown on the right within squares. See also Figure S7 for results considering other spatial distributions of departing birds

to falcons during September and consequently on the falcons' annual productivity (Fitted model: productivity = 2.05 − 3.51e$^{(-0.000015 \times \text{prey})}$, $p = 0.008$, $R^2 = 0.70$, Figure 4c). In addition, variations in wind patterns during September caused strong fluctuations in food availability, leading to periods of food shortage (Figure 5). The duration of these periods (food gap) was an even stronger predictor of annual productivity (Fitted model: productivity = 2.74 − 0.21 × food gap, $p < 0.001$, $R^2 = 0.86$, Figure 4b, see also Table S1 and Figure S6 for results corresponding to other distributions of departing birds). Finally, positive NAO values during September were also associated with high falcons' productivity values ($t = -7.35$, $df = 3.18$, $p = 0.004$).

4 | DISCUSSION

This study is a comprehensive example of how climate interacts with local demography to determine population fitness and viability. The mechanistic approach taken allowed us to unravel the cascading effects of the annual fluctuations of a major climatic phenomenon over the Atlantic on the vital rates of a wild bird population, and provided the first evidence of wind as a major determinant of a vertebrate's population fitness. Both the field data and the simulation model independently support that the variability of trade winds determines food availability for Eleonora's falcons during the reproductive season, being a key driver of their breeding success on the Canary Islands, their western and southernmost population. Unravelling the complete mechanism underlying the falcons' breeding success allowed us to link processes operating at very different spatial scales, the broad-scale climatic driver and the local-scale population processes.

Over the decade of the study, the productivity of Eleonora's falcons was determined by the Atlantic trade winds. These winds originate from large-scale atmospheric circulation dynamics in the Atlantic Ocean, and are associated to the NAO. In general, positive

NAO phases are associated with strong trade winds, whereas negative phases result in weaker winds (Azorin-Molina et al., 2018). The NAO index was generally associated with the breeding success, which reinforces the idea that annual productivity is directly linked to large-scale climatic conditions. However, productivity was best explained by the intensity of easterly winds measured along the migration pathway of bird prey.

Easterly winds finely determined the availability of migratory birds as prey, regardless of the intensity of the migratory flux from the Iberian Peninsula (Figure 2). Indeed, wind is known to affect bird migration. For example, long non-stop flights of up to 37–48 hr to cross the Sahara desert have been proposed as a possible strategy for many migrants heading to the African savannahs (Adamík et al., 2016; Ouwehand & Both, 2016), but the migration efficiency is highly dependent on wind due to a trade-off between tailwind assistance and the risk of drift by crosswinds over northwest Africa (Erni, Liechti, & Bruderer, 2005). Similarly, easterly winds that are encountered in the middle of the journey to Africa cause many migratory birds to reach the Canary Islands instead of Africa. A large proportion of the birds that are hunted by falcons near the Canary Islands are inexperienced juveniles (up to 95%), which are more prone to drift when confronted with crosswinds (Bäckman & Alerstam, 2002; Mouritsen & Larsen, 1998). Although Eleonora's falcons adjust their hunting effort according to the prevailing wind regime (see also Ristow, Wink, & Wink, 1983; Rosen, Hedenström, Badami, Spina, & Åkesson, 1999; Viana et al., 2016; Walter, 1979), this does not compensate for low prey availability when extreme adverse wind conditions occur. In times of prolonged food shortage, male falcons reach the African continent for self-maintenance, leaving females and nestlings behind. During these periods, some nestlings die of starvation, whereas others are cannibalized by neighbouring adult females (Gangoso, Afán, Grande, & Figuerola, 2015), thus reducing offspring production. For example, in September 2014, the lack of easterly winds led to long periods of food shortage (up to 11 consecutive days, see Figure 5), which resulted in total chick mortality. Complete breeding failure has been reported in other species (e.g. Ropert-Coudert et al., 2015; Xavier, Croxall, & Reid, 2003) and its frequency is likely to increase and spread due to the impact of extreme weather conditions and spatiotemporal predator–prey mismatches (Durant et al., 2003). The consequences of demographic variability for long-term population growth can be enormous (Boyce et al., 2006; Sæther & Bakke, 2000), and although the effects of losing entire cohorts are unknown, climatic impacts could reduce reproductive output below stable population levels (van de Pol et al., 2010) and lead populations to undergo risky demographic stochasticity (Gomulkiewicz & Holt, 1995).

The trajectory model provides a reliable tool for predicting the breeding performance of this falcon population, which when linked to a demographic model, can allow the forecasting of population growth under a changing climate. Other mechanistic models that explicitly incorporate processes such as physiology, reproduction, dispersal or adaptation have proven useful in predicting population responses to climate change in predators [e.g. polar bears *Ursus maritimus* (Molnár et al., 2010); Eurasian golden plovers *Pluvialis apricaria* (Pearce-Higgins et al., 2010)] and primary consumers [e.g. greater gliders *Petauroides volans* (Kearney, Wintle, & Porter, 2010)]. However, future climate scenarios relevant to the ecology of Eleonora's falcons are highly uncertain. Alongshore trade winds may have strengthened during the last few decades because of global warming (Bakun, 1990), while more local predictions, such as for the Canary region, are equivocal (Sydeman et al., 2014). Global model projections indicate that there will be latitudinal differences in coastal wind trends during the 21st century that are mainly associated with shifts in the seasonal development and geographical positions of major atmospheric high-pressure systems, such as those affecting trade winds (García-Reyes et al., 2015; Rykaczewski et al., 2015; Wang, Gouhier, Menge, & Ganguly, 2015).

Just as wind has been a key factor in facilitating the colonization of the Canary Islands by Eleonora's falcons, by pushing their prey in that direction, a change in wind patterns could also cause their local extinction. Within the archipelago, Eleonora's falcons only breed on the northernmost and easternmost islets, which are the closest to the African mainland and where passerines arrive in the highest numbers. This population at the edge of the species' breeding range is, therefore, highly vulnerable to changes in the North Atlantic climatic system. If the hunting effort of these falcons cannot keep the pace in a scenario of altered migration patterns due to changing winds, local extinction is highly possible. Extinction of the Canarian population would cause a range contraction and consequent loss of intraspecific behavioural and genetic variation, with evident consequences for the conservation of this species. Still, it is also important to consider that different mechanisms may prevent population declines in the face of changing climate. Even though these falcons have limited alternative food resources at the Canarian breeding areas (Gangoso et al., 2013), they can still change the timing of breeding, disperse to more favourable areas or adapt through ecological and evolutionary responses that can occur over short timescales (Mills et al., 2018; Vedder, Bouwhuis, & Sheldon, 2013; Visser & Gienapp, 2019). Having a predictive model of population fitness will be the basis for accurate forecasting of population trends when reliable climatic models become available.

Although wind regimes explained the productivity of the Canarian population of Eleonora's falcon, the question remains whether the relative simplicity of this system applies to other populations. The species breeds across the Mediterranean basin and, although all populations depend on the flux of migratory birds to raise offspring, the importance of wind might vary depending on the geographical location of the colonies with respect to migratory flyways. To understand the consequences of changes in wind patterns at the species level, it would be necessary to simultaneously compare the performance of different colonies, such as those from the Canary Islands and Mogador (Essaouira, Morocco, which is located only 1.5 km far from the mainland), as a function of wind conditions. It seems reasonable to assume that populations closer to the mainland will be less affected by wind conditions because migratory birds

can be more accessible. Indeed, falcons breeding on the Canary Islands visit the mainland under prolonged periods of food shortage (Figure 2b).

In general, the importance of wind regimes might be underappreciated, as the population dynamics of other species might be largely dependent on wind-driven resources. For example, the breeding colonies of many seabird species are sustained by marine resources made available through oceanic currents and coastal upwelling influenced by wind regimes (e.g. Schmidt et al., 2015), or wind is in itself a driver of foraging success (e.g. Cornioley, Börger, Ozgul, & Weimerskirch, 2016). Under unfavourable wind conditions, the energetic costs of foraging flights at sea during the breeding season may be too high as to impact population-level demographic processes, such as reproduction and survival (mostly of young individuals; Frederiksen, Daunt, Harris, & Wanless, 2008; Hennicke & Flachsbarth, 2009; Thorne et al., 2016; Weimerskirch & Prudor, 2019), and even increase the risk of extinction of some populations (Hass, Hyman, & Semmens, 2012). Therefore, changes in wind regimes may affect the future distributions of wind-dependent bird species. For example, the foraging range of wandering albatrosses *Diomedea exulans* has shifted poleward over the past decades due to parallel changes in westerly winds in the Southern Ocean (Weimerskirch et al., 2012).

5 | CONCLUSIONS

We demonstrate that understanding the mechanisms underpinning population fitness can be key for predicting population dynamics under environmental change. Our approach greatly benefited from deploying information on many different aspects of the ecology and life history of the study species. While detailed knowledge of life history and ecology cannot be produced for every species, it has been crucial for understanding the breeding performance of Eleonora's falcons and formulating solid working hypotheses in the first place. We advocate that this approach can be valuable for the conservation of targeted species such as emblematic and keystone species. Detailed mechanistic understanding and consequent predictive ability is key knowledge for local conservation initiatives, and can serve as the foundation upon which we can scale up to study environmental change impacts at the species level. We also highlight that climate is not only about temperature and precipitation but also includes other important facets, such as wind, that can have major roles in the ecology and maintenance of many populations and species.

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AUTHORS' CONTRIBUTIONS

L.G., D.S.V., J.F. and W.B. conceived the study and devised the methodology; L.G., D.S.V. and S.A.B. collected the data; L.G., D.S.V., A.D. and W.B. analysed the data with input from J.S.-B. and J.F. L.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

GPS and radar data and the R and Matlab codes used to perform the statistical analyses and the trajectory model, respectively, are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0rxwdbrx5 (Gangoso et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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